1.—Variation, Classification and Evolution in Flowering Plants— with particular reference to Thysanotus

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The sources of variation in flowering plants are briefly discussed and illustrated by examples from the genus *Thysanotus*. In two species— *T. patersonii* and *T. tuberosus*—evidence of variation is presented which supports the establishment of sub-specific taxa. The occurrence of intra-specific polyploidy is reported and compared from the point of view of geographical distribution with other selected Australian genera.

The world distribution of the tribe Asphodelae in terms of its constituent genera and the distribution of the species of *Thysanotus* are considered in the light of Willis' Age and Area theory and of a recent hypothesis of Smith White. A hypothetical evolutionary history of the genus *Thysanotus* is presented.

This address will be concerned with plant systematics and will indicate the various lines along which research into what may in general be called "the species problem" has been conducted and how the results from such investigations have affected the science of flowering plant taxonomy and thrown light on pathways in evolution.

In systems of classification of flowering plants there had grown up from the time of Linnaeus (1753) the idea that each individual species was an invariable entity and out of this concept arose the use of the "type"—a single plant specimen located in some particular herbarium which provided a fixed reference point and which, taken in conjunction with the written description of the species, enabled subsequent workers to identify plants of the particular taxon. This may be an unfamiliar word to some of you—it means a particular taxonomic entity at whatever level is under discussion, for example—species, genus, etc.

Over the last thirty years concurrent with the rise of genetics as a science there has been a marked increase in the interest taken in variation in plants and as a result there has developed what has variously been called the "new systematics" (Huxley 1940), "experimental taxonomy" (Clausen, Keck and Hiesey 1941) and "biosystematy" (Camp and Gilly 1943). The results from such investigations have not so far resulted in a change in the orthodox taxonomic methods nor in a rejection of the type system, although various authors as for example Gilmour and Gregor (1939) and Gilmour and Heslop-Harrison (1954) have suggested a nomenclatural system which would assist in codification of the various categories among plants recognised as a result of experimental taxonomic investigation.

The point of departure between what has been called "classical" or "alpha" taxonomy and experimental taxonomy is the attention paid to the variability of the plant species as a result of intrinsic and extrinsic factors. The interrelationship of the two approaches is shown in Table I modified from Heslop-Harrison (1953).

In order that we may better understand the relationship between these two approaches let us look first at some of the sources of variation in the flowering plant. Most people are familiar with the basic cell of which the complete structure of the plant is made up. It is a complex assemblage of inorganic and organic chemical compounds in an aqueous medium contained within a membrane enclosed by a cellulose cell wall. Among the important organic chemical compounds are proteins, ribose nucleic acid (RNA) and desoxyribose nucleic acid (DNA). The proteins are important because of their part in building the fine structure of the cell and their association with the enzyme system. Together with the nucleic acids just mentioned they form nucleoproteins of which DNA-proteins make up the genetic units of the cell—the chromosomes—which can be made visible by suitable methods, and RNA-proteins make up microsomes in the cytoplasm and also form other so far invisible (except in the electron microscope) cytoplasmic bodies. Genetics has established that the chromosomal part of the genetic system is distributed in a regular fashion by meiosis prior to the formation of embryo sacs and pollen grains and that at this stage in the life history there is the possibility of variation in the genetic constitutions of the various products of meiosis. Here then we have the first method by which variation can occur.

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TABLE I

The relationships of "classical" and "experimental" taxonomy (after Heslop-Harrison 1953)

	CLASSICAL TAXONOMY	EXPERIMENTAL TAXONOMY
AIMS	Description, classification and naming.	Identification of evolutionary units, determination of genetical relationships.
UNIT OF STUDY	Individuals, usually dead.	Breeding population, or a sample from it, living.
SYSTEM OF CLASSIFICATION	Basic unit the species, fitted into a hierarchical system.	Classification not the primary aim, basic units vary.
SOURCE OF DATA	Morphology, anatomy plus notes on flowering time and geographical distribution.	Morphology, anatomy, karyology, life cycle details, effects of habitats, genetical tests.
TESTS OF CHARACTERS	Intuition and trial and error.	Statistical methods.
METHODS OF DESCRIPTION	Individuals and "type" concept.	Populations or samples of populations.
CONCEPT OF NATURAL VARIATION INVOLVED	Essentially static, assumes continuity of form within species.	Essentially dynamic, internal variability of sexual populations is recognised, adaptive nature of much population differentiation acknowledged and made deliberate object of study.

Whether the process of meiosis always results in variation depends upon the genetic state of the organism, whether it is homozygous or heterozygous and also on the breeding system of the plant. With regard to the latter there are three possibilities, (1) inbreeding (or self-pollination), (2) outbreeding, or cross-pollination) and (3) apomixis—a single term covering a number of possible variants of the sexual process. To deal with the last of these first—apomixis is a mechanism which results in the elimination of variation resulting from meiosis and conversely the maintenance of variation occasioned by means other than meiotic recombination. An extreme form of apomixis is the replacement of sexual reproduction by vegetative propagation.

To return to the first two, the choice between in- or out-breeding may be controlled by either the floral morphology of the plant or a specific part of its genetic make-up, or possibly both. As an example the pea flower is anatomically designed for self-fertilisation since the stigma is receptive at the time of anthesis, and also in close proximity to the anthers. The cleistogamous flower of the violet—since it never opens —also ensures self-fertilisation. On the other hand distylous flowers—types of flowers which are found with two possible lengths of style alternating with two possible anther positions—are spatially arranged to encourage cross-pollination by insect visitors as for example the primrose *(Primula)* and loosestrife *(Lythrum)*. In some of these cases the anatomical mechanism is reinforced by a genetical system of incompatibility genes.

Of anatomical mechanisms for ensuring cross-pollination may also be mentioned the system in some members of the Compositae (the daisy family) in which pollen is shed into a central tube and released to visiting insects as a result of the style growing up through the tube. When the style has grown beyond the limits of the tube the divided apical parts of the style recurve and expose the inner receptive surfaces of the stigma which then becomes receptive to other pollen. Genetic systems for ensuring cross-pollination are based on the "S" gene series which, by means of interaction between pollen carrying a specific allele of the series and diploid stylar tissue carrying the same allele results in retardation or complete inhibition of the growth of the pollen tube or even inhibition of pollen germination upon such stigmas. Other methods are known which achieve the same end as for example in the evening primrose *(Oenothera)* in which both ovules and pollen grains containing particular genetic combinations (the so-called Renner complexes) do not develop. This is a system of gametic lethals; alternatively where particular zygotic genetic combinations do not develop, a system of zygotic lethals is found.

What then can be said from the point of view of variation about the results of the various breeding systems just mentioned? Apomixis will tend to reduce variation, or if variation results from mutation it will perpetuate it without change—it is therefore a system which imposes restrictions upon the variability of the plant possessing it. Obligate self-pollination will result in homozygosity after relatively few generations, since from inbreeding a heterozygote followed by self-pollination of all the progeny (neglecting any form of selection for a particular genotype) the proportion of heterozygotes: homozygotes becomes progressively 1:1, 1:3, 1:7, etc. Put in another way the proportion of heterozygotes in such a population would be represented by $(\frac{1}{2})^n$ where n = number of generations of inbreeding. We see in this a very rapid reduction in the number of heterozygotes in such a population. Only with outbreeding is there the possibility of segregation and recombination and thus the persistence of heterozygosity. We therefore expect that the self-fertilised species will possess little or no genetic variation within its populations derived from a single individual whereas the outbreeding species will show marked variability.

So far we have been concerned with genetic variation, which is controlled by the chromosomally-borne genes. The whole chromosome complement of the plant may be altered by the incidence of polyploidy—in the simplest case the duplication of the chromosomal set to produce a tetraploid. This increase in chromosomal material may or may not show itself in the

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morphology or physiology of the plant. There is a great deal of literature now available on this topic and one may generalise to the extent that increase in size of various parts, for example flowers, frequently coupled with reduction in fertility, often occurs following polyploidy.

Variation may also arise from environmental factors. This was thought at one period to be the reason for the identity of allied species and claims have been made that by transplanting individuals from their normal habitat to another they could be shown to be transformed into another species typical of the new habitat. The experiments of Bonnier (1895) were claimed to show the transformation of lowland species into alpine ones. Due to lack of careful cultivation methods and keeping of accurate records, the results from these experiments are now viewed with suspicion. Subsequently the transplantation technique has been used by such workers as Turesson in Sweden, Gregor in Scotland and Clausen, Keck and Hiesey in California. Not only have reciprocal transplants been used, but the concept of growth under uniform environment of plants from diverse ecological situations has been extensively used. The use of this approach under most critically controlled conditions has been in the use of what have been termed "phytotrons"—each consisting of a collection of rooms with either natural or artificial lighting in which strict control of day and night temperatures, humidity and day length is possible. Under such conditions it has been shown by Went (1953) in the case of the Earhart Laboratories in California that variation due to environment can be virtually entirely removed and that as a result genetical experiments which would normally require many replications to ensure statistical accuracy can be conducted with very few plants. This type of apparatus provides an ideal site for researches into physiological differences between races of plants as for example the work of Hiesey (1953) on *Achillea*.

The sources of variation have now been mentioned, but what of their effect upon the plant species? Genetic variation may provide sharply discontinuous morphological changes as for example in flower colour. A very common example of this is the mutation to white flowers in a species normally possessing coloured flowers. In *Thysanotus* this has been found in several species, e.g., *T. triandrus* (Shearer, personal communication), in *T. tenuis* near Tinkurrin, Western Australia, and *T. tuberosus* at Virginia, Queensland. In most cases the change to albinism is complete and affects all parts of the flower. In the case of the Tinkurrin plants however, there seem to be two stages each presumably controlled by a separate gene. In one of these the anthocyanin pigment is absent from the perianth parts but remains in the anthers (which in this and most other *Thysanotus* species are normally purple coloured); in the other, anthocyanin is absent both from perianth and anthers, the latter then appear green. Mutation of the normal pale purple flower colour to a salmon pink has also been seen in a population of *T. tuberosus* in southern Queensland.

A presumed mutational effect which concerns the morphology of the perianth in *T. patersonii* is reported from localities in northern South Australia and southern Northern Territory. In this case the fringed margin to the inner perianth segments is absent and led Black (1943) to use the manuscript name of var. *exfimbriatus* for such plants. Live material has recently been obtained from a population of this plant through the courtesy of Mr. Paul Wilson of the South Australian State Herbarium and it is hoped in the forthcoming season to be able to determine whether environment changes the expression of this character. By experimental cross-pollination with normal fringed types it is hoped to be able to determine the genetical relationship between the normal and the exfimbriate form.

Genetic variation may also result in continuous as opposed to discontinuous morphological variation giving the so-called quantitative variation shown mostly in characters such as the overall size of plant parts. This aspect of plant variation has been extensively studied by the Californian workers Clausen, Keck and Hiesey (Clausen 1951). The results shown in Figure 1 are a sample of the type of results obtained when plants from various localities on a transect across California are grown under uniform conditions at the Carnegie Institute experimental plots at Stanford, California. Each plant shown in the figure represents the mean of the population from that locality and the histograms show the variation within that population. If individual plants from such populations are selected and vegetatively propagated by means of ramets and grown under identical conditions at each of three localities, results such as those shown in Figure 2 can be obtained. This shows that the responses of genetically different plants are quite different at the three localities and that among the vertical lines of plants which represent the ramets derived from a single individual, there are marked differences in the response of the plant to the environment at the three localities used in the experiment. At any one particular habitat the sum of the variation adds up to the total variation shown by the histograms in the previous figure.

As a result of these approaches together with experimental crossing of races from different geographical and ecological habitats it has been possible to elucidate the genetical and physiological bases for the observed morphological differences among members of a particular species.

As yet no extensive experiments of this sort have been carried out with *Thysanotus*—some transplanting to a more or less uniform environment in a Perth glasshouse has been undertaken and progeny have been raised from seed derived from selfed parents. From the latter the indications are that there is little variation in such characters as size of plant within the progeny. This lack of variation in sexually produced progeny would lead one to suspect that the plant was most likely to be normally self-fertilised in nature.
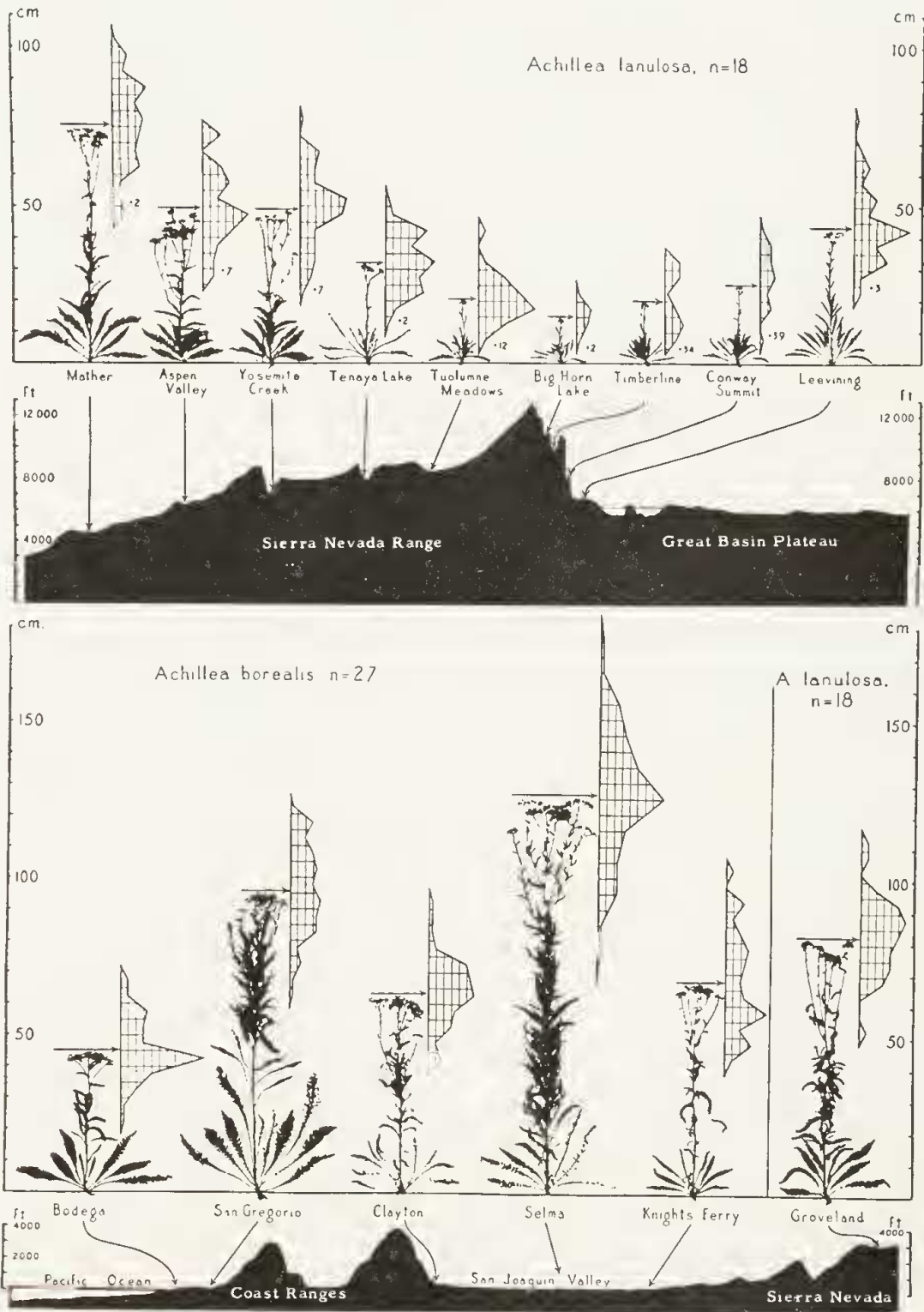
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Fig. 1.—Altitudinal climatic races of *Achillea* from a west-to-east transect across central California. The frequency diagrams indicate variation in height within the populations in the Carnegie Institution plots at Stanford, California. The plant specimens represent the means. (after Clausen, Keck and Hiesey 1948.)
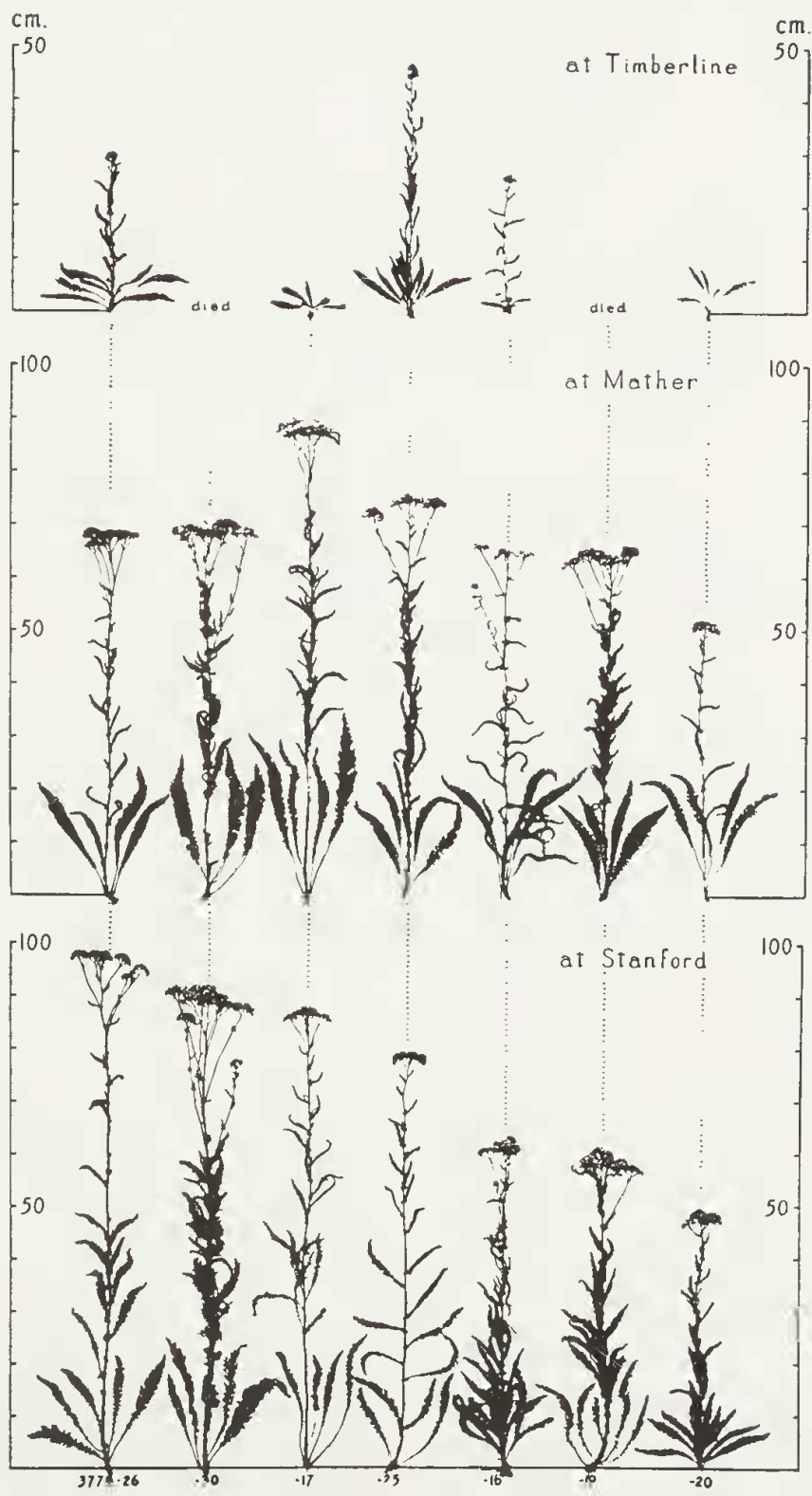
Fig. 2.—Responses of seven cloned individuals taken from a population at Mather (alt. 4,600 ft.) when transplanted to the environments at Stanford, Mather and Timberline. (after Clausen, Keck and Hiesey, 1948.)

Here we may make a digression to look at the floral morphology of the plants. The flowers are either three or six stamened and typically the anthers are curved and tend in the open flower to lie with their apices near the terminal stigmatic part of the style. In the majority of the species the anther opens by a terminal pore and it is thought that there is a "pepper pot" pollination mechanism in these cases. Such a mechanism does not provide large quantities of pollen loose in the flower. In a few species the anthers open by longitudinal slits and in these cases there is much more pollen freed at any one time. In these latter cases also there is close proximity of style and anther and pollination by direct mechanical transfer of pollen is suspected. Insects are hardly ever seen visiting the flowers and emasculated non-bagged flowers in a glasshouse in the vicinity of other open non-emasculated flowers of the same species do not set seed. The evidence therefore suggests self-fertilisation as the normal condition for the plant.

If instead of considering variation in height on an intrapopulation basis we look for interpopulation variation within the species we find examples of this in *T. triandrus* and *T. multiflorus*. In the former species the variation was such that Domin (1913) erected a series of varieties of which the smallest—from the vicinity of Youndegin (35 miles east of York, Western Australia) had been given specific rank by Ewart and White (1908) as *T. bentianus*. If these variations in height are plotted geographically a positive correlation appears between decrease in height and decrease in annual rainfall. It would seem that in this case we have a cline—defined as a gradual transition in a characteristic associated with geographical or ecological change. A similar pattern emerges from a study of height in *T. multiflorus* which shows reduction in size correlated with progressively south-western distribution. These variations may be merely plastic responses to the environment, this can be proved or disproved only by determining whether the height typical of the original population is maintained when plants are grown under more or less uniform conditions. If changes of environment do not bring about changes in the height of the plants the genetical control of the character is demonstrated. If it is possible to select types morphologically different from others in the cline the term ecotype of Turesson could be applied to such plants. Ecotypical variation implies that genetic modification has occurred in response to the environment with modification in some characters as for example size, but not to the extent that the plants showing this variation should be placed in different taxonomic groups. The work of Silsbury and Brittan (1955) demonstrated the existence of ecotypical variation in *Kennedya prostrata*.

As a general rule it is to be expected that if a species covers a wide geographical range, which is therefore likely to include several different ecological conditions together with the possibility of isolation into small populations there is greater likelihood of the development of infraspecific categories. In *Thysanotus* the two most widely ranging species are *T. tuberosus*

and *T. patersonii*. The former has a distribution which ranges from Cape York and northern Northern Territory through Queensland, New South Wales, Victoria and to the east of the Mount Lofty Ranges in South Australia. The typical form over this range has flowers with perianth segments 11-19 mm long, six stamens —of which three have short (3-3.5 mm), more or less straight anthers and three with long (6-9 mm) curved anthers. The longer ones are comparable in length to the style. This floral morphological pattern is constant over most of the range but may be accompanied by variation in overall size and vigour of the plants. In the area around Brisbane and possibily south into New England there occurs a distinct form with perianth parts 7.5-9.5 mm long, six stamens almost equal in length—three with anthers 2.5-3 mm long, three with 3-5 mm anthers— arranged more or less parallel to the open perianth parts. The differences were first recognised in live material sent from Brisbane through the courtesy of Dr. Blake and Mr. Coaldrake. The morphological differences were found to persist in cultivation. In an attempt to elucidate the relationship between these types artificial cross-pollinations between them have been attempted. The results to date show that both types are self fertile and that crossings in which the large flowered form is the female result in no seed production, whereas the reciprocal (small flowered female) sets seed. So far plants have not been raised from such experimental crosses.

During an extended collecting trip in 1959 I was able to examine several habitats for *T. tuberosus* near Brisbane. Plotting the occurrence of the two types gave a distribution in which the types replaced each other without obvious reason at intervals in a north-south direction (the sampling having been carried mostly along the Brisbane-Maryborough road which runs more or less north-south). The area is mostly occupied by "wallum"—coastal plain country on which grows *Banksia aemula* and *Melaleuca leucadendra* (sensu lato). There are slight altitudinal variations of the order of 100 feet, the lower parts tending to be waterlogged. From the study of the distribution of the two types the pattern emerges that on the lower wetter parts the smaller flowered type is found and that with increase in elevation it is replaced by the larger flowered type. In an area of c. 300 × 10 yards at Beerburrum both forms were found in ratios varying from 8:0 (large:small) to 1:9 over the area. Again the higher proportion of the smaller flowered type was found on the lower parts. The sampling was obviously confined to the plants in flower at the time and does not represent a complete sample of the population. It demonstrates that the two types are distinct and are able to maintain their identities in a mixed population. It is proposed on the basis of the evidence presented to separate the types at the subspecific level, the large flowered one to be known as *T. tuberosus* subsp. *tuberosus* and the smaller flowered type as *T. tuberosus* subsp. *blakei*. In the same tuberous-rooted, paniculate inflorescenced group Robert Brown (1810) described *T. elatior*—a taller, more robust plant with

larger flowers collected from the north coast of Queensland and islands in the Gulf of Carpentaria. Similar plants have been found by me in inland New South Wales and although no experimental work has been done it is thought that the morphological variation does not merit specific rank and that until the results of investigations are known such plants should be included within the subspecies *tuberosus*.

By comparison with the distribution of *T. tuberosus* which shows a mainly north and south trend, the distribution of *T. patersonii* shows largely an east-west trend occurring as it does in southern New South Wales, Victoria, Tasmania, South Australia, southern Northern Territory and extra-tropical Western Australia. It is worth noting that on present knowledge it is the only widespread extra-tropical *Thysanotus* species recorded from eastern and western Australia, in addition it is the only species so far recorded from Tasmania, whence the type specimen was collected. Kunth in his Enumeratio (1861) delineated the species *T. manglesianus* based on a specimen collected from New Holland by Captain Mangles, in the course of the description mention is made that a specimen collected by Gaudichaud from the Vasse River (near Busselton, Western Australia) is identical with the type. Subsequent workers as for example Baker (1877) have submerged *T. manglesianus* within *T. patersonii*. One of the distinctions made by Kunth was the larger flower size in his specimens compared to Brown's type specimens from Tasmania. My researches have shown that in addition to larger flower size the anthers of the inner and outer whorls of stamens are dissimilar in size, whereas those in *T. patersonii* (sensu stricto) are nearly equal in length. An additional morphological character is the form of the ripe capsule which in the small flowered forms has an overall length of *c.* 5 mm and has the persistent perianth parts free at the tips whereas in the large flowered form the overall length is *c.* 13 mm of which *c.* 8 mm is made up of the persistent perianth parts closely appressed and slightly twisted together. The size of the capsule itself in the two forms is almost the same. The two forms are found growing in nearby localities in Western Australia, but so far no evidence has been obtained of the presence of intermediates. As mentioned above some species of *Thysanotus* possess anthers which dehisce by longitudinal slits, *T. patersonii* is one of these and as a result of the larger amounts of pollen shed it is less likely that cross-pollination between types would occur in this species. I therefore propose to re-establish *manglesianus* as an epithet at the subspecific level to describe the large flowered, western form of *T. patersonii*. The small flowered plant as exemplified by Brown's Tasmanian collection becomes *T. patersonii* subsp. *patersonii*.

In *T. patersonii* it has also been possible to demonstrate the existence of polyploidy—the occurrence in plants of chromosome numbers greater than the typical diploid number which for *Thysanotus* is 22. A chromosome count of *c.* 80 was reported on Tasmanian material (Jackson, unpublished data) and subsequently in association with Jackson I was able to show that this was 88—the plant would therefore be termed an octoploid. There is in this case no morphological difference from other plants of *T. patersonii*, we therefore have an example of a chromosome race whose identification is only possible from microscopic examination rather than from macroscopic examination—the latter the more normal technique in herbaria. So far no chromosome numbers intermediate between diploid and octoploid have been found, one would expect that—unless they had been lost in the evolutionary process—there would be tetraploid types in existence. Live plants have been obtained from various localities in Tasmania and northward on the mainland towards Newcastle, N.S.W.—which seems from herbarium records to be the northernmost limit for the species in eastern Australia. Cytological investigation of these plants may, it is hoped, provide evidence of the existence of the tetraploid race. A similar situation of chromosome polymorphism without morphological differentiation has been found by James (unpublished data) working on Western Australian populations of *Isotoma*.

Hagerup (1932) stated that in the Northern Hemisphere more northerly populations possess a higher proportion of polyploids. Subsequent workers who analysed the Spitsbergen flora were however not able to substantiate this point. Manton (1937) working on a crucifer *Biscutella laevigata* which had been found to possess diploid and tetraploid races in Europe, showed that the distribution pattern was such that the tetraploid occupied the areas which had most recently been freed from ice and that the diploid remained in the lower altitudes. This was held to show that the more recently evolved tetrapoid possessed the ability of more rapidly colonising new habitats. Other workers have subsequently found evidence from other plants which agrees with this interpretation. It may well be that in the case of *T. patersonii* an ancestral diploid (or possibly tetraploid) form migrated across the then existing Bass Isthmus and that under glacial conditions in Tasmania these forms were replaced by higher polyploid forms and themselves failed to survive. That the octoploid is not recent in origin is suggested by the regularity of its meiotic division and the possession of high fertility. It would seem that the process of "diploidisation" had gone on with the production of regular meiosis and the restoration of fertility. The possible alternative would be that another species of *Thysanotus* was able to hybridise with the ancestral form and that from a putative sterile hybrid the present octoploid was developed by chromosomal doubling. The possible objection to this latter theory would be that some trace might be expected of introgression (Anderson 1949) of characters from the other parent and one would expect a difference in morphology between the octoploid and its mainland relatives. This has not so far been observed.

The last example I wish to quote from *Thysanotus* is the case of the two species *T. triandrus* and *T. multiflorus*. They are both solely Western Australian in distribution and both belong to the section of the genus possessing only three stamens. They are similar in

habit, they have fibrous, non-tuberous rooted stocks surrounded by leaf bases both current and past, the leaves are without petioles and erect. The scape is simple and has a single terminal umbel of flowers. The distinguishing characters of the two species are *T. triandrus*—leaves linear-lanceolate. channelled. covered with a more or less dense tomentum; *T. multiflorus*—leaves linear, flat, glabrous. In the latter species luxuriant specimens may develop a second sessile or shortly stalked inflorescence some distance below the terminal one. Experimental cross-pollination between the species produced seed and subsequently a mature plant. The hybrid is somewhat intermediate between the parents; it has the flat linear leaves of *multiflorus* which develop a tomentum similar to that of *triandrus*. Only a single plant reached maturity and rather than use the buds for cytological investigation, experimental self- and back-cross pollinations were carried out. No seed was obtained from either of these experimental crossings. From results so far one can tentatively conclude that in spite of the production of a viable hybrid plant there is either insufficient homology in the two chromosome sets or that breakdown occurs in the development of endosperm, leading to the failure to produce viable seed. If this is the true picture it means that should intercrossing take place in the field the production of hybrid individuals does not automatically mean the production of hybrid swarms and the subsequent possible breakdown of the species boundaries. Such an intercrossing is not very likely under natural conditions since the parents are ecologically isolated— *T. triandrus* is found on the sandy soils of the coastal plain and the inland sand plain, whereas *T. multiflorus* is distributed through the eucalypt forest on the lateritic soils of the Darling Range. There are areas in south-west Western Australia where *T. multiflorus* tends to occur on sandy soils but in these areas *T. triandrus* is absent. If future experimental self-pollination of hybrids between the two species results in the production of mature seed and subsequently plants, one would then be justified in reducing the two parental species to the status of sub-species of a single species. since the possibility of their being able to exchange genes would have been demonstrated.

A second case of polyploidy has been found in the genus—within *T. multiflorus*, here at the tetraploid level 2n 44. Two localities are known for plants which on morphological grounds would be referred to *T. multiflorus*. but which occur on the coastal plain associated with swampy conditions, one near Welshpool and the other near Pearce. In each locality *T. triandrus* occurs in the vicinity. The tetraploid plants are fertile and possess a regular meiotic division. Taking the cytological and morphological evidence together it could be postulated that polyploidy here is a case of amphidiploidy— the doubling of the chromosome number in a sterile diploid hybrid. possibly similar to the one between *T. triandrus* and *T. multiflorus* to which reference has already been made. So far attempts to obtain seed from experimental crosses between the tetraploid and its putative parents have been unsuccessful. Another line

of attack is the possibility of artificially doubling the chromosome number of the experimentally produced hybrid and then checking the product against the naturally occurring 2n 44 plant. This would be a similar method to that used by Müntzing (1930) who was able to synthesise from the two diploid species of *Galeopsis* an amphidiploid which agreed very closely with the naturally occurring *G. tetrahit* whose origin had been hypothetically attributed to a cross between the ancestors of the two diploid species used in the experimental cross. Under such experimental conditions one cannot expect exact duplication of the existing form because of the time lapse which occurs between the original and the experimental cross which allows of possible evolution in the parental genotypes.

The cytological situation as it affects the evolutionary pattern of the Angiosperms in Australia has been recently reviewed by Smith White (1959) who commences by considering separately the woody and non-woody types of plants with Australian and extra-Australian distributions. After study of the available chromosome numbers of hardwood genera of families such as Myrtaceae, Proteaceae, part of Rutaceae, Epacridaceae and Casuarinaceae he finds that within Australia there is marked diversity in chromosome numbers compared with extra-Australian members of these groups and that this diversity is at generic rather than specific level. At the species level polyploidy is rare and number variations are unknown within species.

In softwood or herbaceous types he finds it difficult to obtain groups of comparable size to those just mentioned. his choice is the families Goodeniaceae and Lobeliaceae and the genera *Danthonia* and *Nicotiana*. Within the two softwood families polyploidy is frequent. reaching levels of hexaploidy and octoploidy in the Goodeniaceae where many cases of intraspecific polyploid series are found. In the genus *Lobelia* different base numbers but no polyploidy are found in the Australian species, whereas extra-Australian species possess a single base number and show polyploidy both at intra- and interspecific levels. *Nicotiana* shows a similar situation to that pertaining in *Lobelia*, there is chromosome number diversity but little polyploidy in the Australian compared to the extra-Australian species. An entirely different situation holds in the grass genus *Danthonia* where, as shown by the data of Brock and Brown (1961) high polyploids up to decaploid level with 2n 120 are found in a series of species which are considered to be primitive as shown by the possession of hairs on the lemma (Table II). Associated with reduction in the number of hairs there is a corresponding rise in the proportion of diploid species and reduction in the maximum level of polyploidy to the hexaploid level.

The other monocotyledons mentioned by Smith White are the grass genus *Themeda* and the liliaceous genera *Sowerbaea* and *Blandfordia*. The two former genera differ markedly in number of species *Themeda* having many and *Sowerbaea* only two. They are similar in the possession of polyploidy, although its geographical occurrence is reversed in the two genera.

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TABLE II

Polyploidy and evolutionary series in species of Danthonia *(after Brock and Brown 1961)*

Lemma hairs	2n = 24	2n = 48	2n = 72	2n = 96	2n = 120
S C A T T E R E D	*linkii* *longifolia* *carphoides* *semiannularis* *occidentalis* 31%	*linkii* & var. *fulva* *longifolia* *clelandii* *geniculata* *richardsonii* 31%	*linkii* var. *fulva* *induta* *pallida* 19%	*induta* *pallida* 13%	*induta* 6%
T W O R O W S	*caespitosa* *setacea* *acerosa* *alpicola* *auriculata* *duttoniana* *monticola* 50%	*caespitosa* *setacea* var. *breviseta* *eriantha* 21%	*caespitosa* *bipartita* *purpurascens* 21%	*procera* 7%	

R E D U C E D	*laevis*
	pilosa &
	  var. *paleacea*
	nivicola
	penicillata
	racemosa
	66%
		laevis
		pilosa &
		  var. *paleacea*
		22%
			laevis
			11%		

In *Sowerbaea* the eastern species is tetraploid and the western diploid. *Themeda australis* according to the data of Hayman (1960) has a diploid distribution ranging from Tasmania to southern Queensland. In the same region there occurs a tetraploid, occasional triploids, pentaploids and three localities for a hexaploid. In the central, western and northern part of the continent the diploid is absent, the tetraploid is widely represented and a single locality for the hexaploid is reported.

The genus *Blandfordia* extends into Tasmania and it is reported that this species is tetraploid, whereas the three species in eastern New South Wales are diploid. This situation parallels to some extent that already reported above for *Thysanotus patersonii* and is the reverse of that reported in *Themeda australis* where only the diploid is found in Tasmania.

Smith White (1959) compared the chromosome numbers of the eastern and western Australian members of the families already mentioned under hardwood types above and found almost exact agreement between them (Table III). This fact he uses as the basis for a theory that the Angiosperms arose outside Australia and then migrated as an already differentiated body from the north. Let us look at the distributional and variational pattern in *Thysanotus* in the light of this theory. A single species is found in the Philippines, China, Siam, Malaya, New Guinea and also in tropical Australia. In New Guinea the presence of *T. tuberosus* is also reported. Of the two species with distributions outside Australia the one with the wider distribution, *T. chinensis,* is a plant with little or no adaptive morphology to life in drier conditions, it has thin mesophyllous leaves and a fibrous root system without tubers. This habit is shared with *T. triandrus, T. multiflorus, T. asper* and *T. glaucus*—all of which are western in distribution. *T. tuberosus* possesses a root system with tubers and although the leaves are mesophyllous they die back and do not have to survive summer conditions. The other Australian species possess either a tuberous root system or an underground rhizome. Of these two types all those with tuberous roots possess aerial parts which die back and are replaced annually, whereas the rhizomatous forms have perennial above-ground parts which may be either leafy or somewhat rush-like.

If we accept Smith White's hypothesis it would require that *T. chinensis* would have been the original form developed outside Australia and that it was waiting—as he puts it— "at the bridgeheads" when migration began. It would seem unlikely that a form with tuberous roots and an annual cycle of leaf renewal would be evolved under tropical conditions in New Guinea; this statement being based on the adaptive value to dry conditions of the root system and also on the lack of the colonisation of the Malay Archipelago by *T. tuberosus.* On the other hand if we require that *T. tuberosus* or some ancestral form of this species evolved in Australia the time during which this could occur is limited by the necessity for a land connection for the northward migration to New Guinea. This theory of the origin of *Thysanotus* conflicts with the view recently expressed by Burbidge (1960, p. 194) that "it would appear that *Arthropodium* and *Thysanotus* may be Australian elements and that they should be recognised as such where they occur outside the region."

If the distribution of the tribe Asphodelae (to which *Thysanotus* belongs) is plotted in terms of the areas occupied by its constituent genera the following pattern emerges—the two biggest genera *Anthericum* and *Chlorophytum* have a wide tropical and sub-tropical distribution, the next largest genera occur in South Africa and Central Asia, *Thysanotus* is fifth in order. If the geographical distribution is looked

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at in terms of number of genera in a given area then the Australian continent with a total of eleven genera has the highest concentration, these are distributed as six occurring in both east and west, three in the east only and two occurring only in the west. South Africa has only four genera, although one of these is the large genus *Bulbine*. Only a few of the genera within the Asphodelae which are represented in Australia are also found beyond it; for example *Arthropodium* is found in New Zealand and New Caledonia, *Herpolirion* in New Zealand, *Chlorophytum* generally distributed in the tropics and *Caesia* in South Africa. If the genera with Australian distributions are plotted on a basis of rough known localities it is found that the largest number of species occur in the south-east and south-west of the continent. If one invokes Willis' Age and Area hypothesis (Willis 1949) the evidence from geographical distribution just presented favours a southern rather than a northern origin for the group.

TABLE III

Comparison of basic chromosome numbers in hardwood genera of eastern and south-western Australia (after Smith White 1959).

Family and genus	Basic numbers	
	South-western	Eastern
Myrtaceae		
Actinodium	6	—
Darwinia	6, 9	6
Homoranthus	—	6, 9
Verticordia	6, 8, 9, 11	—
Boronieae		
Zieria	—	18
Boronia		
valvatae	16	16
terminales	9	9
pinnatae	11	11
Eriostemon	14	14
Phebalium	16	16
Proteaceae		
Persoonia	7	7
Grevillea	10	10
Hakea	10	10
Conospermum	11	11
Isopogon	13	13
Petrophila	?	13
Adenanthos	13	—
Lambertia	14	14
Banksia	14	14
Dryandra	14	—
Epacridaceae		
Styphelia	4	4
Astroloma	4	4, 7
Conostephium	8	—
Melichrus	—	8
Leucopogon p.p.	4	4
Leucopogon p.p.	6	6
Leucopogon p.p.	11	11
Brachyloma	7?	9
Acrotriche	9	9
Lissanthe	—	7
Monotoca	—	12
Andersonia	12	—
Sprengelia	—	12
Lysinema	12	—
Epacris	—	13
Woollsia	—	13
Richea	—	13
Dracophyllum	—	13
Sphenotoma	6, 7	—
Casuarinaceae		
C. glauca group	9	9
C. distyla complex	11	11

If we look at the Australian distribution of *Thysanotus* species we find that in common with such genera as *Banksia* and *Hakea* the genus is predominantly western, twenty-six species being found in south-west Western Australia compared to five in south-eastern Australia. The section triandrae with the reduced number of three stamens is restricted to Western Australia. Of species which occur in both east and west mention has already been made of *T. patersonii* and *T. chinensis*, in addition *T. tenellus* although mainly western is found in South Australia. There are however examples of what may on further investigation prove to be vicarious species pairs as, for example *T. tuberosus* and *T. thyrsoideus: T. juncifolius* and *T. pseudojunceus.*

Evidence for a much wider distribution of *Thysanotus*, at least in Western Australia is provided by the occasional occurrence of very disjunct populations of the two species *T. dichotomus* and *T. sparteus*. Both species are normally restricted to the *Eucalyptus marginata-E. calophylla* forest (the Jarrah forest) of the Darling Scarp. *T. sparteus* has a slightly wider distribution and is also found on the coastal plain with *E. gomphocephala* (Tuart) and *Banksia menziesii*. Isolated occurrences of these *Thysanotus* species are found associated with granitic outcrops in what is now the Western Australian wheat belt. None of these localities has specimens of *E. marginata* and curiously the one locality (Jilakin Rock) with Jarrah has not so far been found to contain *Thysanotus*. Gardner (1944) in "The Vegetation of Western Australia" makes a special category of plants associated with the habitat provided in the vicinity of these outcrops, which provide a higher level of soil moisture as a result of the runoff from the rocks.

If we attempt to reconstruct the history of *Thysanotus* we could—following Smith White—postulate an invasion from the north by *T. chinensis* which did not go very far south in eastern Australia but reached further in Western Australia: secondly the evolution of tuberous rooted forms either simultaneously in east and west or at a single locality followed by migration: thirdly migration of a tuberous rooted form to New Guinea: fourthly the development of plants with rhizomatous rootstocks and the lack of formation of root tubers (this again needs two centres of origin or migration from a single centre): fifthly the development of climbing forms and the migration of these to Tasmania—the absence of other species from Tasmania requires either a limitation of southward migration or the complete destruction of immigrants during the period postulated above for the production of the Tasmanian polyploid *T. patersonii*: sixthly the evolution of the three stamened species in Western Australia followed by: seventhly further speciation in Western Australia to account for the larger number of species in that region. Future work on relationships of somewhat similar—morphologically speaking—eastern and western species may help to decide between the alternatives given in the second and fourth stages, further work with

populations of *T. patersonii* should help solve the problems mentioned under the fifth heading.

In summary then we may say that a study of variation in *Thysanotus* provides evidence of variation at single gene mutation level (flower colour); the occurrence of intraspecific polyploidy *(T. patersonii)*; the occurrence of subspecific variation maintained by partial genetic barriers and by the pollination mechanism *(T. tuberosus* and *T. patersonii)*; the presence of ecologically isolated species which have diverged to the extent of being able to produce sterile hybrid progeny, with which is associated the possible production of an amphidiploid *(T. triandrus* and *T. multiflorus)* and also the presence of ecotypes in clinal form *(T. triandrus* and *T. multiflorus)*.

A postulated pattern of invasion and speciation is suggested based on Smith White's hypothesis, posing however the question as to the possibility of a migration at a later date of one species in the reverse direction. Much work still remains to be done on this and many other similar and related problems before the picture of the evolution of the Australian flora will be in any way complete.

Acknowledgments

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